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Diversification patterns and size evolution in caviomorph rodents

ALICIA ÁLVAREZ[1]*, R. LETICIA MOYERS ARÉVALO[2] and DIEGO H. VERZI[3]

[1]*Instituto de Ecorregiones Andinas (INECOA), Universidad Nacional de Jujuy, CONICET, Instituto de Geología y Minería, Av. Bolivia 1661, Y4600GNE San Salvador de Jujuy, Jujuy, Argentina*
[2]*Unidad Ejecutora Lillo (UEL: FML-CONICET), Miguel Lillo 251, T4000JFE San Miguel de Tucumán, Tucumán, Argentina*
[3]*CONICET. Sección Mastozoología, Museo de La Plata, Paseo del Bosque S/N°, B1900FWA La Plata, Buenos Aires, Argentina*

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Caviomorph rodents are one of the most diverse mammalian groups in the Neotropics; they display astonishing eco-morphological variation, including unparalleled size range. Here we analyse evolutionary patterns among extant caviomorphs, particularly their rates of diversification and size evolution. The results show large heterogeneity in the evolutionary dynamics of caviomorphs. Three clear episodes of rapid increase of the diversification rate were detected; two of them during the Oligocene were related to the diversification of major clades; a third one, in the late Miocene, was related to the diversification of the genus *Ctenomys*. Regarding size, relatively low rates characterized much of Octodontoidea, the most speciose among the main caviomorph clades. Other clades, especially Cavioidea and Chinchilloidea, showed much accelerated evolutionary rates and the highest number of size changes, particularly increases; furthermore, they include extinct representatives that reached very large to gigantic size. Thus, although the macroevolutionary dynamics of caviomorphs were complex and heterogeneous in our study, the pathways followed by different clades seem to display their own particular characteristics. This should be analysed in greater depth through new, greater scale analyses incorporating the rich fossil record of caviomorphs, which contributes essential information to understand the evolution of these peculiar rodents.

ADDITIONAL KEYWORDS: caviomorph rodents – divergence times – evolutionary diversification – molecular phylogeny – size evolution.

INTRODUCTION

Caviomorphs are the most ecomorphologically diverse clade of rodents, evolved primarily in South America at least since the middle Eocene. They are first recorded in the middle Eocene of Contamana, Peru (*c*. 41 Myr; Antoine *et al.*, 2012), through scarce isolated molars whose affinities to extant clades remain the subject of controversy (Vucetich *et al.*, 2015). A richer fauna from the late Eocene of Santa Rosa, Peru (Frailey & Campbell, 2004), and taxa from the Late Eocene–early Oligocene de Tinguiririca, Chile (31.4–35.6 Myr; Bertrand *et al.*, 2012) already evidence the divergence of the four major extant clades, that is Cavioidea, Erethizontoidea, Chinchilloidea and Octodontoidea. The fossil record suggests pulses of diversification and extinction, the most important of which took place in the middle–late Miocene and gave rise to the differentiation of the extant lineages (Pérez & Pol, 2012; Vucetich *et al.*, 2015; Verzi *et al.*, 2016). In the extant fauna, caviomorphs comprise nearly 250 species distributed among 52 genera and ten families (Patton, Pardiñas & D'Elía, 2015; Wilson, Lacher & Mittermeier, 2016). Throughout their wide distribution along essentially Central and South America, caviomorphs inhabit quite varied habitats including sand dunes, humid and arid steppes (Pampas), dry tropical forests (Cerrado, Chaco, Caatinga), Amazonian rain forests and the High Andean Puna (Patton *et al.*, 2015; Wilson *et al.*, 2016). This is reflected in their

*Corresponding author. E-mail: alvarez.ali@gmail.com

wide-ranging habits (arboreal, epigean, cursorial, semiaquatic, fossorial, subterranean; Nowak, 1991; Emmons & Feer, 1997) and their high morphological disparity (Vassallo & Verzi, 2001; Candela & Picasso, 2008; Morgan, 2009; Álvarez, Perez & Verzi, 2011; Álvarez *et al.*, 2015). A striking feature that characterizes this clade is the unparalleled size variation, especially if the fossil record is considered. Some extant octodontid species weigh as little as 50–80 g (Wilson *et al.*, 2016), while the largest extant rodent, the capybara *Hydrochoerus*, weighs ~50 kg (Mones & Ojasti, 1986). Several extinct large to gigantic cavioids, and especially chinchilloids, including dinomyids and neoepiblemids, reached ~700 kg or even above a ton (Sánchez-Villagra, Aguilera & Horovitz, 2003; Blanco, 2008; Vucetich *et al.*, 2015).

The large taxonomical richness and impressive ecomorphological diversity (especially size variation) of caviomorphs make them an excellent model for studies attempting to understand processes involved in the biological diversification. In this sense, several efforts have been made to disentangle the evolutionary patterns of these peculiar rodents (e.g. Pérez & Pol, 2012; Álvarez, Perez & Verzi, 2013; Arnal & Vucetich, 2015; Upham & Patterson, 2015; Verzi *et al.*, 2016), but the analyses presented in this work are the first to assess the rates of diversification and phenotypic trait evolution. We generated a time-calibrated phylogeny for caviomorph rodents and used a Bayesian framework for estimating those rates. The main goal is to elucidate potential associations between taxonomical and morphological diversification and generate information on the history of caviomorph diversity.

METHODS

Calibrated phylogeny

The sequences for four mitochondrial genes that include the ribosomal subunits *12S* and *16S*, cytochrome b (*cytb*) and the *cytochrome c oxidase subunit I* (*COI*), and five nuclear genes including the growth hormone receptor (*GHR*), interphotoreceptor retinoid-binding protein (*irbp*), recombination activating gene 1 (*RAG1*), transthyretin gene (*TTH*) and the von Willebrand factor (*vWF*) were obtained for 190 species of hystricognath rodents (plus one sciuromorph species as outgroup) obtained from GenBank (accession numbers are listed in Supporting Information S1). Among them, 174 corresponded to caviomorph species. For the selection of sequences, we considered those that were represented in at least 20% of the total number of species. The sequences were carefully depurated, eliminating those that caused artefactual alignments or showed unusual positions in previous exploratory (partial) analyses. The alignment and concatenation of the nine genes into a unique matrix of 10 073 bp were performed using BioEdit (Hall, 1999). Each locus was considered as an independent partition in the phylogenetic analysis. Once the total phylogeny was retrieved, a partial phylogeny including only caviomorphs was used in further analyses.

Phylogenetic relationships and divergence time among taxa were estimated through Bayesian inference methods implemented in BEAST 2.3.1 (Drummond & Rambaut, 2007; Suchard & Rambaut, 2009) accessed via the CIPRES Science Gateway (Miller, Pfeiffer & Schwartz, 2010). The analyses were performed using Markov chain Monte Carlo (MCMC) simulations for five independent runs with 150 000 000 generations and a sample frequency of 10 000. We used a relaxed molecular clock to model substitution rate variation among branches (Drummond *et al.*, 2006; Drummond & Rambaut, 2007) and the Birth-Death speciation model. We ran BEAST analysis with 'unknown rate' for gene evolution, so we asked BEAST to estimate them; we used a unique (linked) clock (as the tree) model for all partitions and different site models (all set GTR but with different invariant proportions). Thirteen fossil calibrations were used for dating nodes constrained as monophyletic (see Supporting Information S2). All taxa mentioned along the text, at species through superfamily taxonomic levels, are currently recognized as monophyletic clades. All fossil constraints were set as minimum hard bounds and lognormal and gamma priors were used to set soft upper bounds. Calibrated nodes were selected to date main divergences near the base of the phylogeny and some others at more internal nodes to get more plausible divergence dates (see Marjanović & Laurin, 2007 and references cites therein). Convergence of the five runs was determined using the program TRACER 1.6 (Rambaut, Suchard & Drummond, 2013) and their combination was achieved using LogCombiner 2.3.1 (Drummond & Rambaut, 2007) after removing 25% of the total sample. Finally, we computed the maximum credibility tree in TreeAnnotator 2.3.1 (Drummond & Rambaut, 2007).

Size data

Data on body size, estimated as body weight, for 165 of the 174 sampled species of caviomorph rodents included in the molecular phylogeny were obtained from the literature (see Supporting Information S3). Most of the missing data were given within Echimyidae, especially *Isothrix* for which only three of the six species have a registered weight. When possible, and in order to account for likely outlier values, data from several sources were collected for each species. Both male and female weight values were pooled into the average weight value of the species.

Diversification rates and evolution of size

To analyse diversification and size evolution rates among caviomorph rodents, we used Bayesian analysis of macroevolutionary mixtures (BAMM) v2.5.0 software (Rabosky, 2014) and the BAMMtools package (Rabosky *et al.*, 2014) for R (R Development Core Team, 2016). Diversification rates were inferred using the function 'speciation-extinction' of BAMM which allows detecting rate shifts (that are assumed to occur from the phylogeny according to a compound Poisson process) along tree branches. BAMM uses reversible jump MCMC (rjMCMC) to do this and to sample distinct evolutionary dynamics that best explain the whole diversification dynamics of the clade (Rabosky, 2014). The analysis involved an rjMCMC run of 100 000 000 generations sampled every 20 000 steps and a burn-in of 10%. Incomplete taxon sampling for caviomorph phylogeny (174 species were sampled; i.e. >60% of total number of species) was taken into account in rate analysis; we estimated the proportion of species present in each family and gives this value to each species (see Supporting Information S4 for setting details).

To analyse body size evolution, we used the function 'trait' of BAMM, similarly to the previously mentioned function, which allows inferring evolutionary rates (for size in this case) and their shifts along the phylogeny. BAMM assumes that the distribution of a trait along a phylogenetic tree reflects a mixture of distinct evolutionary regimes that are shared dynamic processes that pertain to subsets of related lineages. Those evolutionary regimes occur across the phylogeny under a compound Poisson process. The method uses rjMCMC to sample mixtures of evolutionary regimes that best explain the distribution of a trait (Rabosky *et al.*, 2014). For this analysis, an rjMCMC run of 500 000 000 generations was carried out; it was sampled every 50 000 steps and a burn-in of 10% was considered (see Supporting Information S5 for setting details). We used a phylogeny pruned from the complete one which included a subset of 165 species for which size data were available (as mentioned above).

For both analyses, that is, diversification and body size evolution, we retrieved the configuration of rate shifts with the highest posterior probability through the 'getBestShiftConfiguration' function of BAMMtools. These configurations were depicted as phylorate plots, which represent the analysed phylogeny with its branches coloured to reflect the instantaneous diversification/trait rate. Additionally, we estimated the rates for selected clades identified by inspecting those phylorate plots. We plotted the cumulative rates through time (from root or the origin of a lineage) for all caviomorphs and those selected clades. We summarized the extent to which species share correlated macroevolutionary dynamics through a cohort analysis. A 'macroevolutionary cohort' is a set of taxa that share a common set of macroevolutionary rate parameters, that is the same evolutionary rate dynamics (Shi & Rabosky, 2015).

To evaluate the detailed evolutionary trend of size variation along the phylogeny, we used a node-by-node approach in the framework proposed by Gould & MacFadden (2004; see Giannini *et al.*, 2012). For this purpose, body size information was incorporated into a tree analysis using new technology (TNT) matrix and mapped as a continuous character onto our dated phylogeny (Goloboff, Mattoni & Quinteros, 2006). Following Giannini *et al.* (2012) and Amador & Giannini (2016), we interpreted nodal location, sign (increase or decrease) and magnitude of change for each node. We recognized four general patterns: stasis (no net change detected in any reconstruction), ambiguity (not reported; discrepant results over reconstructions), increases and decreases. The magnitude of change refers to the net amount of mass increase or decrease common to all possible reconstructions in a given branch. We quantified all net changes within caviomorphs and looked for macroevolutionary patterns in body mass variation in terms of phyletic or apomorphic gigantism or nanism (see Gould & MacFadden, 2004). A phyletic change is considered to occur when two or more consecutive branches present the same sign of change. In contrast, an apomorphic change refers to an isolated change or one with a contrary sign at adjacent ones. The persistence of the phyletic pattern was defined following Amador & Giannini (2016), who stated the order of phyletic change as a simple metric measure that refers to the number of consecutive branches making up the phyletic pattern (which may present from two up to four intermediate branches with no net change); so the higher the order, the more persistent the pattern.

RESULTS

Calibrated phylogeny

The phylogeny obtained is the most complete time tree of caviomorphs at the species level (Fig. 1; Supporting Information Fig. S1 shows the complete phylogeny). Even so, it includes <70% of the recognized species. The topology of the maximum clade credibility phylogenetic tree obtained through Bayesian methods was mostly congruent with previous phylogenies and reinforces a current macrosystematics scheme that is becoming progressively more stable (Galewski *et al.*, 2005; Opazo, 2005; Upham & Patterson, 2012, 2015; Pérez & Pol, 2012; Voloch *et al.*, 2013; Voss, Hubbard & Jansa, 2013; Corrêa Tavares, Pessôa & Seuánez, 2016; Fabre, Patton & Leite, 2016; Verzi *et al.*, 2016),

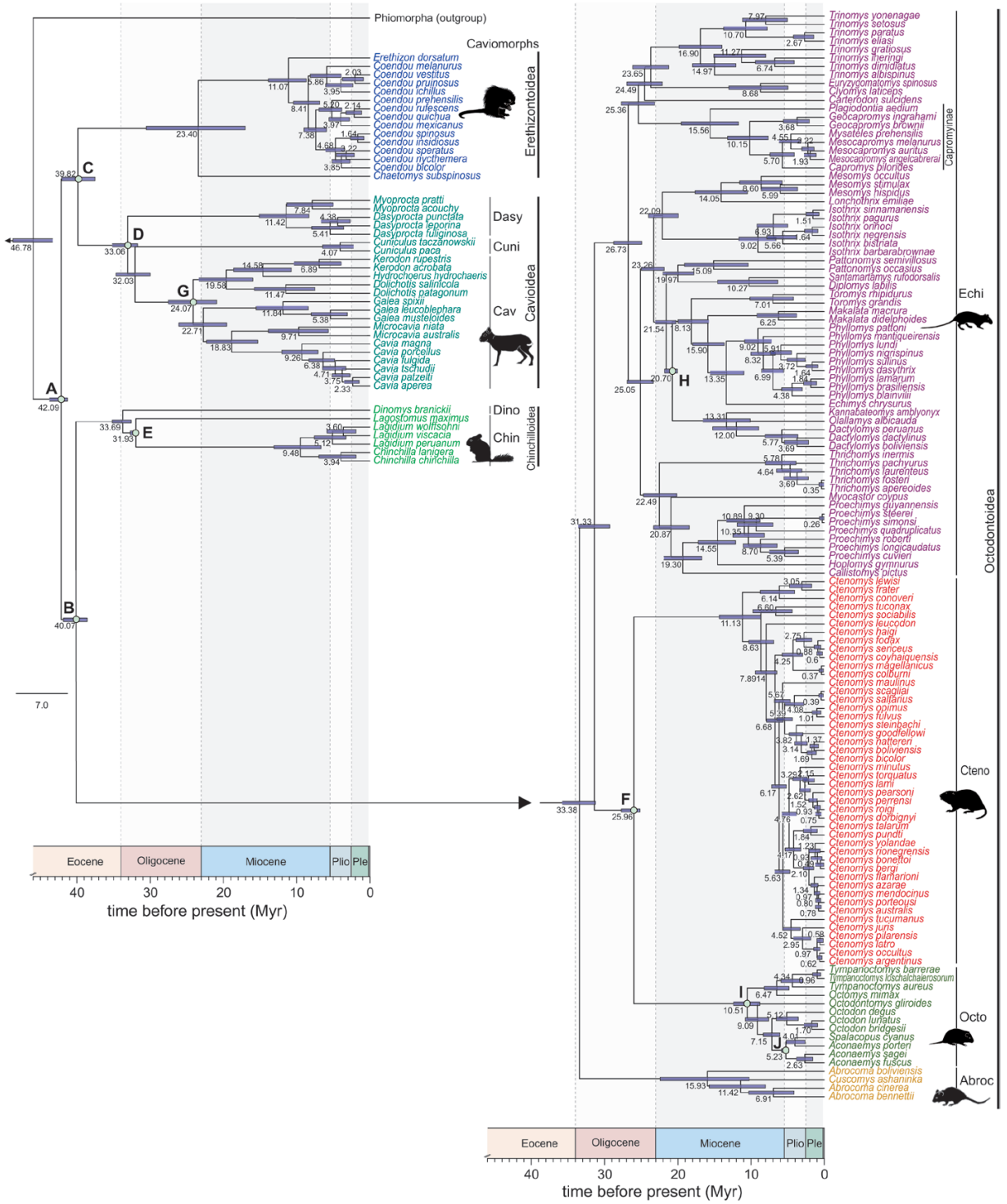

Figure 1. Calibrated phylogenetic tree of caviomorph rodents obtained through Bayesian analysis of a set of nine genes (see main text). Node numbers and bars indicate estimated ages (in Myr) and 95% credibility intervals for each node. Abroc: Abrocomidae; Cav: Caviidae; Chin: Chinchillidae; Cteno: Ctenomyidae; Cuni: Cuniculidae; Dasy: Dasyproctidae; Dino: Dinomyidae; Echi: Echimyidae; Octo: Octodontidae; Ple: Pleistocene; Plio: Pliocene. Nodes A-J represent calibrations constraints (see Supplementary Information S2 for details). Phiomorpha, other hystricognath and sciuromorph rodents were included in the tree construction although their relationships were not illustrated here (see Supporting Information Fig. S1); the arrow at the base of tree indicates the presence of other outgroups besides Phiomorpha.

with some major differences regarding internal relationships among species of the genus *Ctenomys* (see Parada *et al.*, 2011; Gardner, Salazar Bravo & Cook, 2014). About 80% of nodes got a support of >0.8 of posterior probability. Divergence among two major clades, Erethizontoidea–Cavioidea/Chinchilloidea–Octodontoidea, and subsequently among the four subclades, is inferred to have occurred in the middle Eocene. The diversification of crown Cavioidea, crown Chinchilloidea and crown Octodontoidea would have begun in the early Oligocene.

Macroevolutionary analyses

Diversification

The BAMM analysis of rate diversification identified 37 distinct shift configurations forming the 95% credible set. The best shift configuration (with posterior probability = 0.16, i.e. the configuration found in 16% of samples) is provided as a phylorate plot in Figure 2A (the whole credible set is depicted in Supporting Information Fig. S2). This configuration showed two rate shifts, one at the node Octodontidae + Ctenomyidae + Echimyidae (Octodontoidea without Abrocomidae) and another at the node Ctenomyidae. Estimated marginal shift probabilities supported this configuration (Supporting Information Fig. S3). Other configurations included one, two, three or four shifts. All of them always included the shifts detected in the best sampled configuration either together or separately. Other shifts occurred at Erethizontoidea (without *Chaetomys*), Chinchilloidea (or in some internal branch) or Octodontoidea (Supporting Information Fig. S2).

According to BAMM estimates of instantaneous speciation rate, these rates tend to increase among caviomorphs, especially in Ctenomyidae (Fig. 2A; the same pattern was observed for extinction rates; Supporting Information Fig. S4). However, if this clade is not considered, the speciation rates get slower and tend to become stationary at around 10 Mya, as depicted in the diversification (speciation)-through-time plot (Fig. 3). The clade Octodontidae + Ctenomyidae + Echimyidae also influences similarly the caviomorph speciation rate along the time curve between 32 and 10 Mya (Fig. 3). In particular, the speciation rate of Echimyidae increases from nearly 26 to 10 Mya.

Cohort analysis showed that Ctenomyidae conforms a unique cohort (Fig. 4A), with its distinctive macroevolutionary dynamics, not shared with other clades. Four other cohorts could be identified: Erethizontoidea + Cavioidea + Chinchilloidea, Echimyidae, Octodontidae and Abrocomidae (Fig. 4A).

Evolution of body mass

The patterns of body size evolution among caviomorph rodents were very complex. In the BAMM analysis,

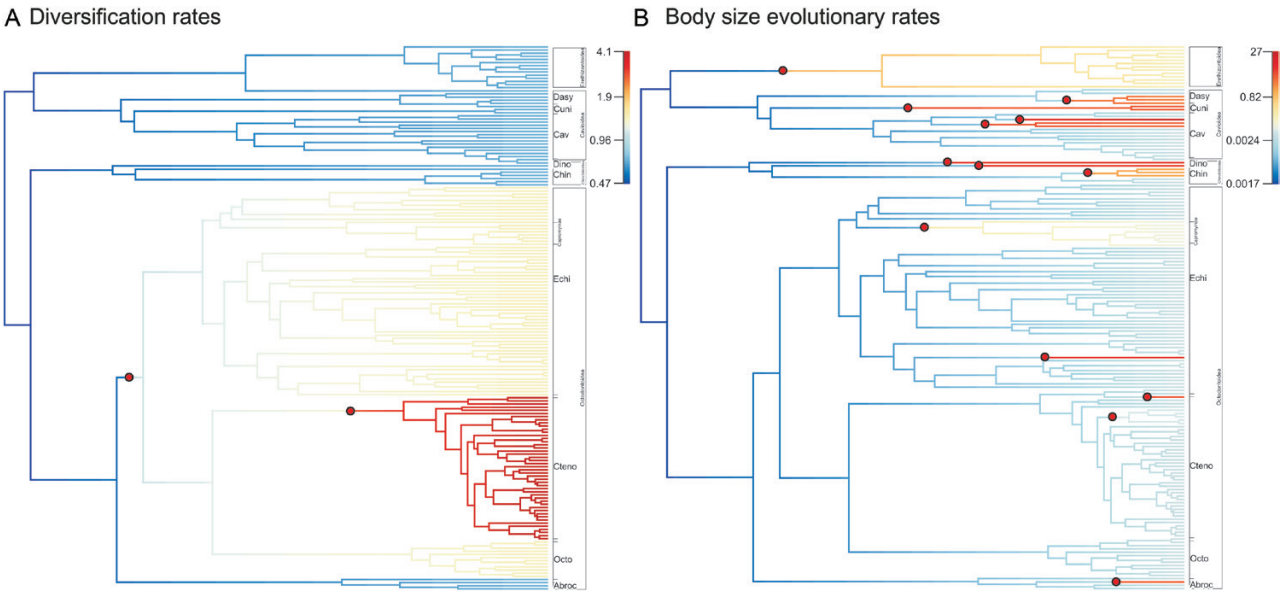

Figure 2. Mean phylorate plot showing (A) mean speciation rates and (B) size evolutionary mean rates. Cold colours indicate slower rates and warm colours indicate faster rates. Log-linear and log-jenks scales were used for colour plotting, respectively. Circles indicate position of macroevolutionary regime shifts detected by BAMM analyses. Abroc: Abrocomidae; Cav: Caviidae; Chin: Chinchillidae; Cteno: Ctenomyidae; Cuni: Cuniculidae; Dasy: Dasyproctidae; Dino: Dinomyidae; Echi: Echimyidae; Octo: Octodontidae.

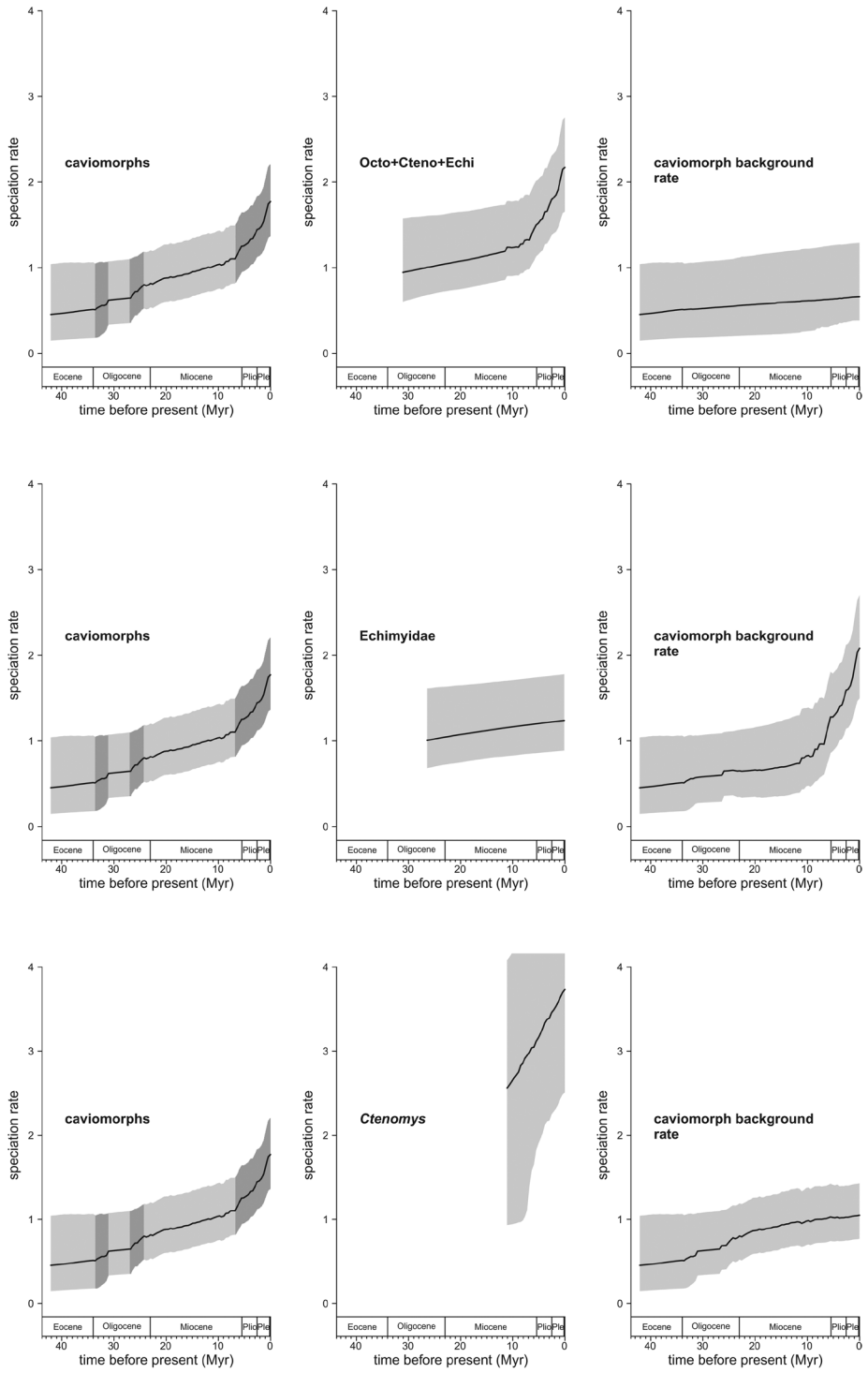

Figure 3. Diversification (speciation) rate-through-time plots. The plots on the left show the cumulative diversification rate from the root of the tree to the present for caviomorph rodents. Three points of acceleration of diversification rate are indicated with dark grey shaded areas. The middle plots show the rate-through-time estimates for the selected clade alone (Octo + Cteno + Echi; Echimyidae; *Ctenomys*, from top to bottom, respectively), and the plots on the right show the background rates for all caviomorphs once the clade has been excluded in the estimation of the rate. Black lines indicate diversification rate curves. Shading around these lines represents 10% through 90% Bayesian credible regions on the distribution of rates at any point in time. Octo: Octodontidae; Cteno: *Ctenomys*; Echi: Echimyidae. Plio: Pliocene; Ple: Pleistocene.

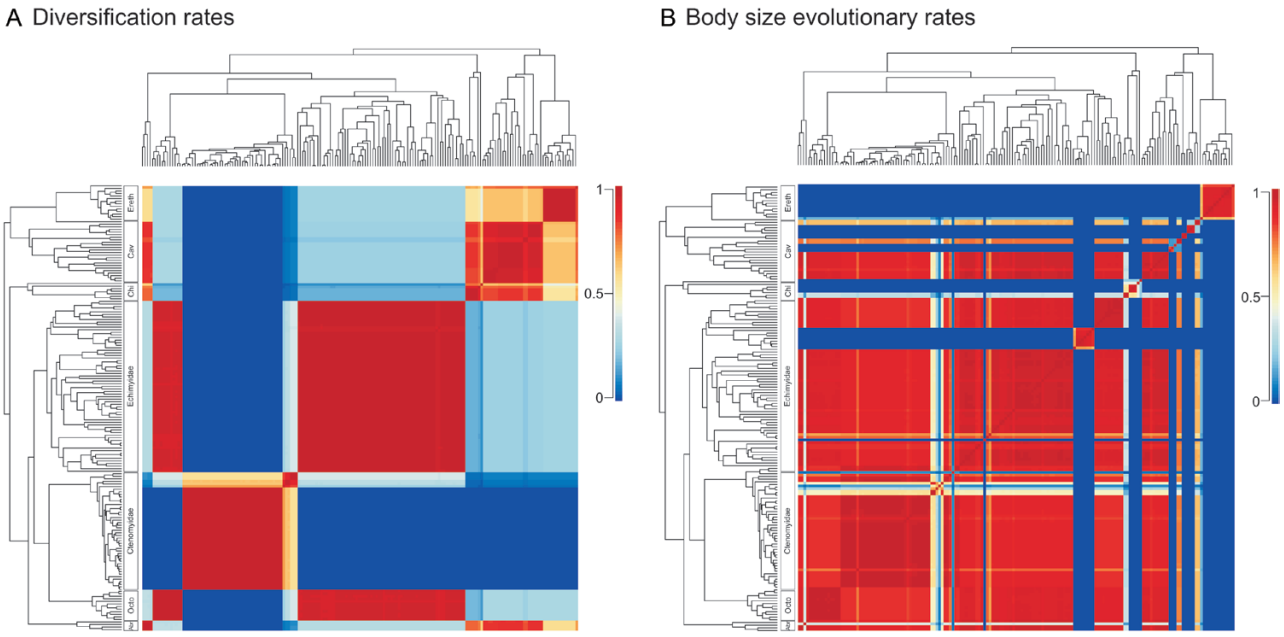

Figure 4. Macroevolutionary cohort matrices for (A) diversification (speciation) and (B) size evolution in caviomorph rodents. The range from cool (0 value on scale) to warm (1 value on scale) colours denotes the probabilities that two species share a common macroevolutionary rate regime. Ereth: Erethizontoidea; Cav: Cavioidea; Chi: Chinchilloidea; Octo: Octodontidae; Abr: Abrocomidae.

6628 distinct shift configurations in the credible set were proposed to explain 95% of data. The best sampled configuration (phylorate plot depicted in Fig. 2B; with 0.0056 of posterior probability) showed a background rate characterized by very low values (dark blue-coloured root and basal branches in Fig. 2B), although there was a tendency to increase of rates; Cavioidea, Chinchilloidea and Erethizontoidea showed the fastest rates (orange-red-coloured branches in Fig. 2B). Size-through-time plots (Fig. 5) showed the increase through time observed in the phylorate plot. The two 'humps' displayed by the caviomorph curve are explained by the behaviour of the rate curves of Cavioidea and Chinchilloidea. Cohort analysis (Fig. 4B) supported the statement of a complex (idiosyncratic) evolution of size, with several clades showing their own rates not shared with any other lineage.

The detailed reconstruction of body mass evolution obtained from the TNT analysis is shown in Figure 6 (also see Supporting Information Figs S5, S6). The total amount of net changes along the caviomorph phylogeny (i.e. the sum of total changes common to all optimizations) was 100.87 kg, of which 93.95 kg correspond to increases and 7.07 kg to decreases (Table 1). The ancestral node of caviomorphs was between 374 g and 1.84 kg; subsequently, there were no net changes along the backbone until the origin of Octodontoidea and Octodontidae, with two consecutive decreases of 92 and 95 g, respectively. The remaining net changes were distributed within each of the main clades. The main increases occurred mostly in terminal taxa, with the greatest absolute increase located at the *Hydrochoerus hydrochaeris* branch (50.06 kg) and two main decreases at the basal node *Chinchilla* (–740 g) and at the [*Galea*(*Microcavia* + *Cavia*)] clade (–714 g). The changes observed in this analysis clearly matched with those observed in the BAMM analysis. In the global pattern and within the groups, the magnitudes of increases and decreases were contrasting. The magnitude of increments was 13 times that of decrements. Most of the net weight increase occurred in Cavioidea (68.45%), while most weight decrease occurred within Octodontoidea (46%).

The summary of net change and stasis frequencies is shown in Table 1. Prevalence of stasis was observed at global level (65%), while the frequency of net increases and decreases was balanced at global level (18.6% and 20.3%, respectively) and within groups (Table 1). In relative terms, considering the size of each main clade (total number of nodes), those with highest frequency of significant changes were Cavioidea and Octodontoidea (38% and 41% of nodes with net change of body mass).

In the terms proposed by Gould & MacFadden (2004), phyletic macroevolutionary patterns were the most prevalent, with a higher frequency than apomorphic ones. This prevailed both at global level and within major clades (Table 2). The most notable cases occurred in the Caviidae and Octodontidae families,

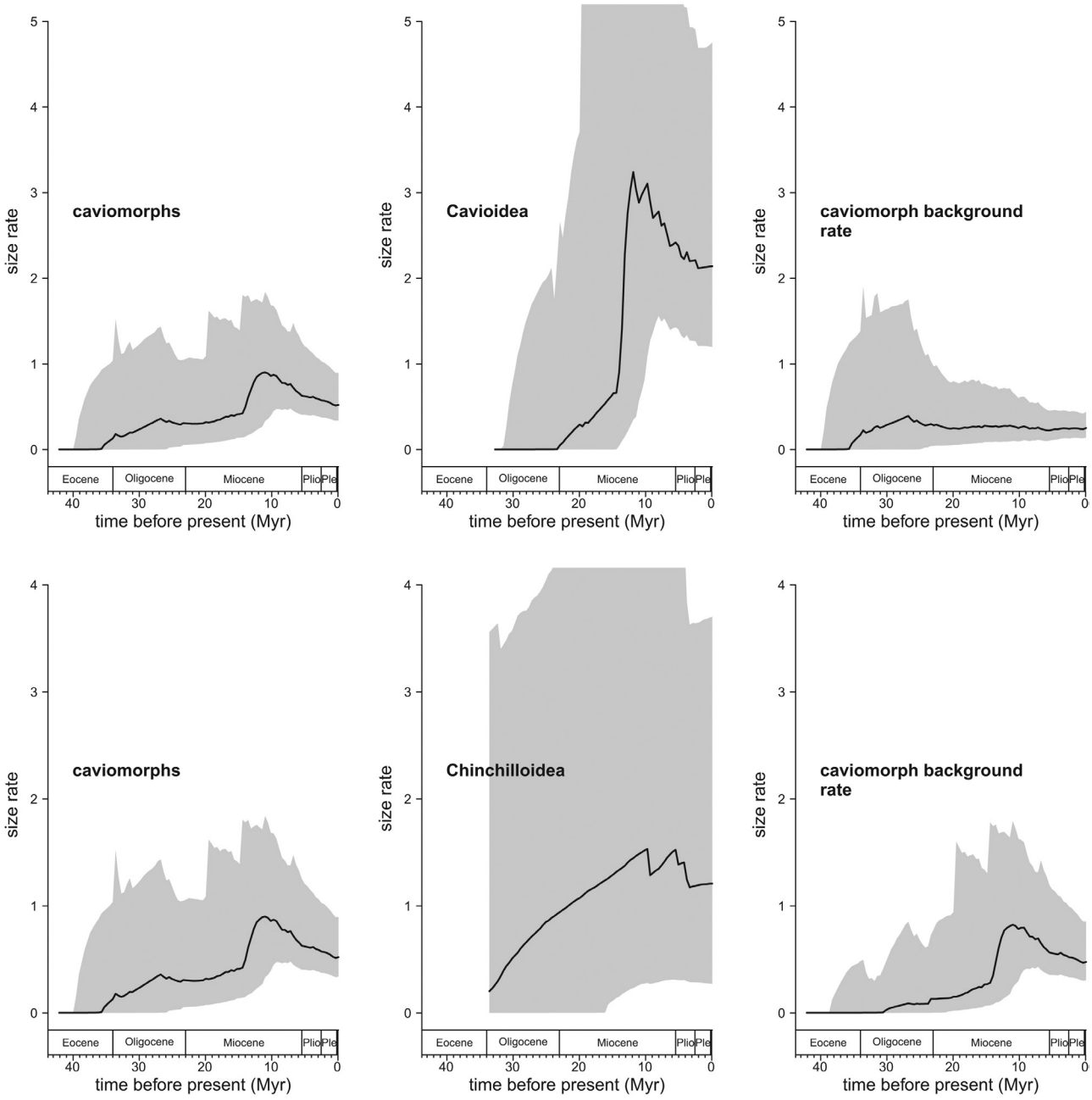

Figure 5. Trait (i.e. size) rate-through-time plots. The plot on the left shows the cumulative phenotypic evolutionary rate from the root of the tree to the present for caviomorph rodents. The middle plot shows the rate-through-time estimates for the selected clade alone (Cavioidea, Chinchilloidea; top and bottom, respectively), and the plot on the right shows the background rates for all caviomorphs once the clade has been excluded in the estimation of the rate. Black lines indicate size evolutionary rates. The shading around lines represents 10% through 90% Bayesian credible regions on the distribution of rates at any point in time. Plio: Pliocene; Ple: Pleistocene.

within which we found cases of third- and fourth-order phyletic nanism, respectively (e.g. the four consecutive decreases leading *Tympanoctomys barrerae*) (Fig. 6; see also Supplementary Information S5 and S6).With respect to the other phyletic pattern, two cases of third-order phyletic gigantism were found, one within Ctenomyidae and another within Octodontoidea (Fig. 6). The remaining phyletic changes correspond to minor patterns (i.e. first or second order) and are spread among groups. Although less common, the

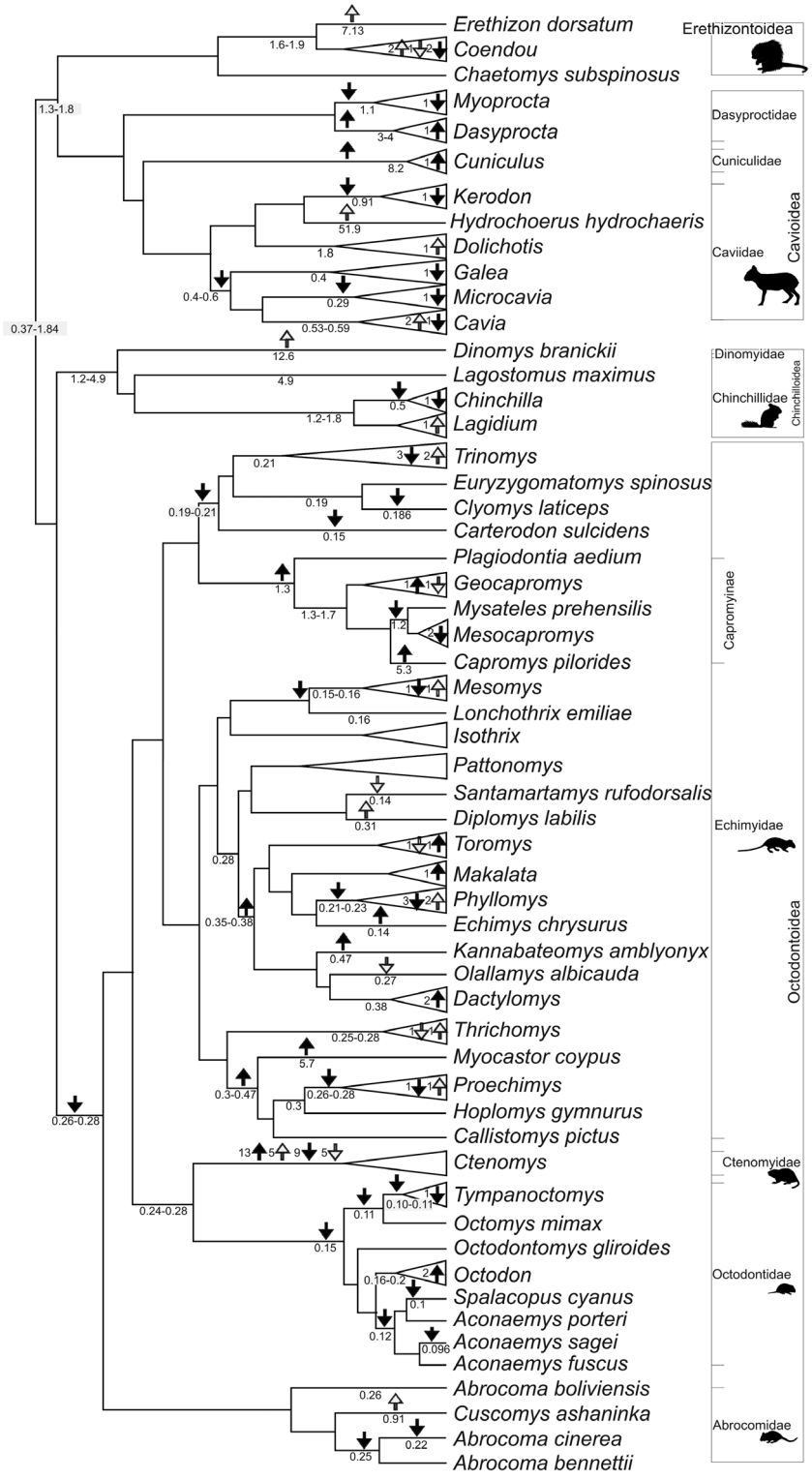

Figure 6. Evolution of body mass in caviomorph rodents analysed through parsimony analysis. Reconstructed values of body mass (kg) are shown below branches. Arrows denote increases or decreases; black ones correspond to phyletic changes and grey ones to apomorphic changes. The number associated to each arrow indicates the number of changes occurred within the corresponding genus.

Table 1. Body size evolution in caviomorphs analysed through body mass optimization on caviomorph phylogeny

Clade	Total number of nodes	Increase magnitude		Decrease magnitude		Stasis frequency		Increase frequency		Decrease frequency	
		a.v. (kg)	%	a.v. (kg)	%	a.f.	%	a.f.	%	a.f.	%
Erethizontoidea	29	7.47	87.2	–1.1	12.8	23	79.4	3	10.3	3	10.3
Cavioidea	45	64.25	97.2	–1.88	2.8	28	62.2	8	17.8	9	20
Chinchilloidea	13	8.71	91.6	–0.8	8.4	9	69.2	2	15.4	2	15.4
Octodontoidea	209	13.52	80.4	–3.29	19.6	121	57.9	42	20.1	46	22.0
Caviomorphs	296	93.95	93	–7.07	7	181	61.1	55	18.6	60	20.3

Magnitude, in absolute (a.v.) and relative terms (%), and frequency, in absolute (a.f.) and relative (%) terms, for each type of net change and for stasis in the main clades of caviomorph rodents.

Table 2. Patterns of body mass evolution in terms of phyletic and apomorphic gigantism and nanism

Clade	Total changes	Phyletic					Apomorphic				
		Gigantism		Nanism		Total	Gigantism		Nanism		Total
		a.f.	%	a.f.	%		a.f.	%	a.f.	%	
Erethizontoidea	6	–	0	2	33.3	2	3	50	1	16.7	4
Cavioidea	17	4	23.5	9	52.9	13	4	23.5	–	0	4
Chinchilloidea	4	–	0	2	50	2	2	50	–	0	2
Octodontoidea	91	28	30.8	38	41.8	66	16	17.6	9	9.9	25
Caviomorphs	118	32	27.1	51	43.2	83	25	20.3	10	8.5	35

Numbers indicate absolute frequency (a.f.) and percentage (%) of changes under the corresponding pattern for each main clade of caviomorphs.

patterns of apomorphic gigantism or nanism are also important in shaping the evolution of this trait, as the case of the branches leading *Hydrochoerus hydrochaeris* and *Dolichotis*.

DISCUSSION

The results obtained in this study showed great heterogeneity in the evolutionary dynamics of the different caviomorph clades. The highest rates of taxonomic diversification (i.e. speciation) were observed within Octodontoidea, particularly in *Ctenomys*, a young highly specious clade whose peculiar speciation pattern has been extensively studied (e.g. Reig, 1989; Lessa & Cook, 1998; Castillo, Cortinas & Lessa, 2005). The plots of speciation through time showed steady increase of this rate for caviomorph rodents, with two 'leaps' in the early and late Oligocene, respectively, and a large increase since the late Miocene–early Pliocene. Several major tectonic and paleoclimatic events could have influenced this macroevolutionary pattern: the global cooling event detected around the Eocene–Oligocene boundary would have been linked to marked faunal turnovers and/or an increase of the diversity of some clades in Europe, Asia and South America (e.g. Prothero, 1994; Goin *et al.*, 2012). Another deepening of the global Cenozoic cooling and drying trend (Zachos *et al.*, 2001), partially combined with local diastrophism corresponding to Andean orogeny (Pascual & Ortiz Jaureguizar, 1990), could have impacted on the diversification rate detected at late Miocene (see Upham & Patterson, 2015). These two turnovers have been recognized in the fossil record of caviomorphs (Vucetich, Verzi & Hartenberger, 1999). Finally, the late Oligocene rate increase could be associated to immigration events to high latitudes of South America (Vucetich *et al.*, 2010).

The increase in speciation rate observed in the early Oligocene coincides with the beginning of the diversification of crown Cavioidea, Octodontoidea, Chinchilloidea and Chinchillidae. The subsequent increase, in the late Oligocene, corresponds especially to the diversification of the crown Caviidae, Echimyidae (and major internal clades), and the splits Octodontidae/Ctenomyidae and Chaetomyinae/Erethizontinae. The marked increase in speciation rate since the late Miocene–early Pliocene coincides with the diversification of genus *Ctenomys*. These results are consistent with the recognition of representatives of three of the four main lineages in

the late Eocene of Santa Rosa (Frailey & Campbell, 2004), and suggest that they should have already been differentiated at the time represented by the Contamana fauna (i.e. middle Eocene; Antoine *et al.*, 2012). In addition, Vucetich *et al.* (2015) recognized radiation pulses in the late Oligocene and late Miocene fossil record of caviomorphs. However, although these results coincide temporally with the rate accelerations detected here, they are strongly incongruous in terms of the clades involved; in particular, the crown groups of Echimyidae, Octodontidae, Ctenomyidae and Caviidae are markedly more recent in the paleontological hypothesis of Vucetich *et al.* (2015; see Verzi, Morgan & Olivares, 2015; Verzi *et al.*, 2016).

In any case, both paleontological and neontological sources of evidence suggest an Eocene–Oligocene radiation for all major caviomorph clades that are already present in the fossil record of this age (Antoine *et al.*, 2012; Bertrand *et al.*, 2012; Vucetich *et al.*, 2015; Boivin *et al.*, 2017). In our analyses the strongest diversification signal was given by Octodontoidea (see Fig. 2a), a highly speciose clade (it includes *Ctenomys* and some speciose genera of Echimyidae such as *Proechimys* and *Phyllomys*; Patton *et al.*, 2015). Moreover, the fossil record of Octodontoidea includes many species, genera and even entire clades that are completely extinct (Arnal *et al.*, 2014; Verzi *et al.*, 2016; Cavioidea shows a similar pattern, see Pérez & Pol, 2012), whose inclusion into the estimates would change the patterns obtained here, probably further increasing speciation rates. Phylogenetic analyses that include both extant and extinct species are necessary for in-depth study of not only speciation but also extinction processes (that are imprecisely estimated from neontological data; see Didier, Royer-Carenzi & Laurin, 2012) that would have greatly affected the diversity of caviomorph rodents and which would have resulted in significant rates of species turnover, as is the case of octodontoids (Vucetich & Verzi, 1999; Vucetich *et al.*, 2015; Verzi *et al.*, 2016).

Evolution rates and patterns of change in body size were also heterogeneous. The backbone of caviomorphs was nearly static (i.e. with no net change; Fig. 6) or presented low rates (see Fig. 2b). Among the main clades, relatively low rates were characteristic of much of Octodontoidea. It has been proposed that decreasing rates are slower than increasing rates in mammals (Baker *et al.*, 2015); in agreement with this result, the decreases of body size prevailed over the increases among Octodontoidea which, in turn, exhibited the greatest magnitude of body mass decrease of all caviomorphs (Table 1). In this regard, octodontoids are unique in retaining a rat-like appearance (Verzi *et al.*, 2016), associated with small to medium sizes. However, rate acceleration was detected for the exceptionally large Echimyidae *Myocastor*, a semiaquatic South American representative, and Capromyinae, a particular clade restricted to the West Indies (Fabre *et al.*, 2014, 2016). Possible insular effect on body size in capromyines remains to be analysed (see Lomolino *et al.*, 2012 and literature therein). Within the family Octodontidae, all net changes are phyletic (mostly decreases, *c.* 78%) and seem to respond to persistent pressures that maintain directional selection over time, presumably at a constant (slow) rate. Most of the members of this clade experienced a significant two to three-fold decrease in body size with respect to their common ancestor with *Ctenomys* (Supplementary Information S5 and S6). Meanwhile, the species of *Ctenomys*, the clade with the fastest diversification, showed similar or only slightly higher rates compared to the background of octodontoids and caviomorphs (see Fig. 2b). However, this genus concentrated *c.* 42% of the total increases and 30% of the decreases estimated for within Octodontoidea, values that may have been achieved with no accelerated rates, excepting for some basal species in this genus (including *C. conoveri*, *C. tuconax*, *C. haigi*, *C. sericeus*, *C. coyhaiquensis*, *C. magellanicus* and *C. colburni*) that showed marked acceleration in the evolutionary rate for their body size. The first two have a northern distribution (Paraguay and Tucumán province, Argentina, respectively) while the others are distributed mostly in Argentinean and Chilean Patagonia. Medina, Martí & Bidau (2007) argued that northern species of *Ctenomys* tend to be the largest ones while southern species tend to show the lowest values for body size (following the converse to Bergmann's rule); if it is the case, our results may reflect geographically restricted changes of this variable through the biogeographic history of this genus which seems to have started in the northern area of its current distribution (Verzi, Olivares & Morgan, 2010; Parada *et al.*, 2011).

Among the remaining clades, the Chinchilloidea, basal Cavioidea (Dasyproctidae, Cuniculidae), caviid subgroups Hydrochoerinae and Dolichotinae, and to a lesser extent, Erethizontoidea, showed much accelerated evolutionary rates and the largest number of size changes, particularly increases which may respond to the fact that an ancestor for all caviomorph rodents with a body mass averaging 1 kg (ranging from 0.37 to 1.80 kg) was reconstructed. This value largely surpasses those estimations accounted for the oldest taxa which would have weighed around 75 g (Antoine *et al.*, 2012). This situation leads to consider the need to include fossils in further analyses on caviomorphs, as was previously discussed for carnivorans and other mammalian clades (e.g. Finarelli & Flynn, 2006; Slater, Harmon & Alfaro, 2012; Puttick & Thomas, 2015). All the caviomorph clades mentioned, at present, include the largest species and most strikingly, several of these groups also had extinct

representatives that reached very large to gigantic sizes, particularly hydrochoerines, and chinchilloids Neoepiblemidae, Dinomyidae and the Antillean heptaxodontid *Amblyrhiza* (Biknevicius, McFarlane & MacPhee, 1993; Rinderknecht & Blanco, 2008, 2015; MacPhee, 2011; Vucetich *et al.*, 2015). These extinct taxa flourished from the late Miocene to Pleistocene; supposedly in relation to various selective factors including newly developed environmental, climatic and ecological conditions (expansion of wide plains and drier climates in areas inhabited by these species; lack of competition and the need to avoid predation; see Vucetich *et al.*, 2015). Following the proposal of Raia *et al.* (2012), caviomorphs would make up an example of how specialization to new niches could promote the emergence of larger sizes, a phenomenon repeated throughout the history of these rodents.

We found that, at least among extant forms, there is a predominance of phyletic over apomorphic changes in body size (gigantism and nanism, following Gould & MacFadden, 2004), partially differing from the patterns found in other groups of mammals (e.g. Chiroptera; see Giannini *et al.*, 2012; and Didelphidae, see Amador & Giannini, 2016), in which phyletic gigantism and apomorphic nanism prevail. This suggests persistent clade-specific trends consistent with directional selection (Amador & Giannini, 2016), for both increases and decreases in body size of caviomorphs. It would be interesting to evaluate the clade-specific patterns in terms of the specific ecological, biogeographical, morphological or morpho-functional features that could drive these evolutionary responses. This is of particular interest among those clades in which the phyletic nanism prevailed, since it constitutes the main difference with other mammals. For this, it would be desirable to re-evaluate the patterns detected in this study while also considering extinct species, for a more accurate estimation of body size and a better understanding of the evolution of this character, one of the most variable among caviomorphs, comprising a 600-fold difference between the average mass of the smallest and largest species of this group (Supporting Information S3). In this regard, several authors have stated that the inclusion of fossil data could play an essential role in elucidating macroevolutionary patterns, especially with respect to body size in mammals (e.g. Finarelli & Flynn, 2006; Slater *et al.*, 2012; Bokma *et al.*, 2016). Although we did not include fossil data, we consider our approach a good approximation to the dynamics of size evolution in this clade. As in Baker *et al.* (2015), the node-by-node approach allowed us to elucidate distinctive paths in the evolution of body size within particular clades. The methods used here prevented us from distinguishing the nature of evolutionary change (in terms of anagenetic vs. cladogenetic changes); however, the detected clade-specific trends such as marked body size increases and accelerated rates for chinchilloids and cavioid subclades, among others, together with clear decreases and slower rates for octodontoids lead us to think that evolutionary changes in body size could be associated to cladogenetic events as proposed by Bokma *et al.* (2016).

Because of the current high diversity (richness) of caviomorphs (only surpassed by cricetid rodents in percentual representation among the non-flying mammalian terrestrial fauna of South America; Patton *et al.*, 2015), and the large number of taxa, which was reached early and maintained along their history (they are usually one of the most abundant clades in fossil deposits; e.g. Montalvo, Tomassini & Sostillo, 2016), caviomorph rodents represent one of the richest groups of the Neotropical fauna, both taxonomically and ecomorphologically. Based on the evidences provided by extant species, and evaluating phenotypic change through size variation, adaptive radiations (see Schluter, 2000; Simões *et al.*, 2016) are not detected in the rise of this diversity. In fact, increases in speciation rates are not accompanied by phenotypic changes in the evolution of extant clades. However, size variation would be linked to the evolution of some clades, such as Chinchilloidea and part of Cavioidea. Remarkably, representatives of these groups acquired advanced hypsodonty very early, in the early and late Oligocene, suggesting that these clades could have been the earliest adapted to open environments and/or abrasive diets (Vucetich *et al.*, 2015; see Mess, Bohr & Thomas, 2001; Mess, 2011). In addition, strong relationship was detected between size variation and morphological variation of the skull related to abovementioned ecological conditions in these clades (Álvarez *et al.*, 2013).

Thus, although the macroevolutionary dynamics of caviomorphs resulted complex and heterogeneous in this study, the pathways followed by different clades seem to exhibit particular characteristics. This should be studied in greater depth by means of new, more comprehensive analyses that incorporate the rich fossil record of caviomorphs, which provides essential information to understand the evolution of these peculiar rodents.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Figure S1. Total calibrated phylogeny, including 190 hystricognath rodent species and a sciuromorph (*Glis glis*) as outgroup.

Figure S2. The 95% credible set of 37 shift configurations from the BAMM diversification analysis of caviomorph rodents. A log-linear scale was used for colour plotting.

Figure S3. Caviomorph phylogeny drawn with branch lengths scaled proportional to the marginal probabilities of rate diversification (speciation) shifts along each branch. The highest probabilities are observed on the branches leading to the clades Echimyidae + Octodontidae + Ctenomyidae and Ctenomyidae. Scale indicates shift probability.

Figure S4. Extinction rate-through-time plots. The plot on the left shows the cumulative diversification rate from the root of the tree to the present for caviomorph rodents. The middle plot shows the rate-through-time estimates for the selected clade alone, and the plot on the right shows the background rates for all caviomorphs once the clade has been excluded. Black lines indicate diversification rates. Shading around the lines represents 10% through 90% Bayesian credible regions on the distribution of rates at any point in time.

Figure S5. Body mass optimization analysis run using TNT software. Terminal values correspond to average body mass (kg) of the species and nodal value corresponds to the reconstructed body mass obtained through the parsimony analysis.
Figure S6. Branch length analysis in TNT. The values shown represent the net changes in body mass (kg) for each node or terminal.
Supporting Information S1. GenBank accession numbers for the genetic (DNA) sequences used for the phylogenetic analysis.
Supporting Information S2. Fossil constraints.
Supporting Information S3. Body size data (weight in grams) used in size evolution analyses.
Supporting Information S4. Setting for BAMM diversification analysis.
Supporting Information S5. Setting for BAMM size evolution analysis.